THE NATURE OF SEXUAL REINFORCEMENT

Lawrence L. Crawford, Kevin S. Holloway,
AND Michael Domjan

UNIVERSITY OF TEXAS AT AUSTIN

Sexual reinforcers are not part of a regulatory system involved in the maintenance of critical metabolic processes, they differ for males and females, they differ as a function of species and mating system, and they show ontogenetic and seasonal changes related to endocrine conditions. Exposure to a member of the opposite sex without copulation can be sufficient for sexual reinforcement. However, copulatory access is a stronger reinforcer, and copulatory opportunity can serve to enhance the reinforcing efficacy of stimulus features of a sexual partner. Conversely, under certain conditions, noncopulatory exposure serves to decrease reinforcer efficacy. Many common learning phenomena such as acquisition, extinction, discrimination learning, second-order conditioning, and latent inhibition have been demonstrated in sexual conditioning. These observations extend the generality of findings obtained with more conventional reinforcers, but the mechanisms of these effects and their gender and species specificity remain to be explored.

Key words: sexual reinforcement, sexual behavior, sexual conditioning, sexual motivation, sex hormones

As the current special issue illustrates, the nature of reinforcement is a major problem of ongoing concern in the experimental analysis of behavior. However, investigators have employed only a small range of reinforcers. In trying to identify general properties of reinforcers, Dunham (1977) commented that, "It is difficult to find much more than the various combinations of lever press, key peck, food, water, and electric shock upon which to base generalizations" (p. 100). The situation has improved little since 1977. Examination of empirical articles using nonhuman subjects published in the last 10 years (1983–1992) of the *Journal of the Experimental Analysis of Behavior* revealed that 85% of the 419 articles reported the use of food reinforcement. Only one article involved sexual reinforcement (Domjan, O'Vary, & Greene, 1988), and only 16 reported the use of a reinforcer other than food, water, or shock. Clearly, thorough investigations of more classes of reinforcers would enable us to make generalizations about the basic nature of reinforcement with greater confidence.

Appetitive reinforcers typically used in studies of animal learning (e.g., food, water, heat) are a critical part of regulatory systems. The ongoing metabolic processes of the organism pose a constant regulatory challenge. Because regulatory systems typically have to be maintained within narrowly acceptable limits, studies of appetitive reinforcers have encouraged the use of regulatory concepts, such as drive reduction, in learning theory (e.g., Hull, 1943). Regulatory concepts have been adopted in more recent behavioral theories, but without explicit reference to physiological mechanisms (e.g., Allison, 1989; Hanson & Timberlake, 1983; Lea, 1978).

Given the emphasis on regulatory concepts in analyses of appetitive reinforcement, examination of appetitive reinforcers that are not clearly a part of a regulatory system would be productive in assessing the generality of reinforcement effects. One such nonregulatory reinforcer is sexual activity. Sexual activity is not necessary for the survival of an individual organism. In species with substantial competition for mates, subordinate individuals may never get to copulate during a breeding season (e.g., Le Boeuf, 1974; McCann, 1981). Sexual behavior may also increase an organism's risk of injury or death from predation or agonistic interactions with conspecifics. Clearly, the benefits that accrue from possibly passing genes to future generations must outweigh these costs.

Phenomena loosely grouped under the heading of "biological constraints" on learning (see, Hinde & Stevenson-Hinde, 1973; Seligman & Hager, 1972) have been a persistent

problem in the development of a general theory of reinforcement. Some (e.g., Bolles, 1985) have considered these effects more problematic than others (e.g., Skinner, 1983). Regardless of the severity of difficulties posed by these phenomena, examination of cases in which the subject's evolutionary history may impose limits on learning may provide an important test of the generality of theories of reinforcement.

A daunting problem facing researchers who wish to find new classes of biologically nonarbitrary learning has been deciding where to look for such phenomena. Most documented cases of biological boundaries on learning have been discovered serendipitously (Domjan & Galef, 1983). A more systematic and fruitful search for such phenomena may be conducted in response systems that exhibit species specificity and diversity and are closely related to reproductive success. Many behavior systems can contribute to adaptation, but sexual behavior is the system most closely associated with genetic transmission. Therefore, studies of sexual reinforcement may be a good place to search for specialized learning mechanisms that have been established by natural selection (Domjan & Hollis, 1988).

OPERANT VERSUS PAVLOVIAN APPROACHES TO REINFORCEMENT

In the following discussion of sexual reinforcement, we consider evidence from studies using both operant and Pavlovian procedures. We follow the conceptualization of Ferster and Skinner (1957) in subsuming both operant and respondent reinforcement under the rubric of "reinforcement." We do not intend to revisit the debate over one- versus two-process learning theories or argue, as did Wetherington (1982), that to attempt to classify some behavior within the traditional operant–respondent dichotomy would be a "theoretical step backwards." For the present review, we concur with Skinner (1983) that, "Whether there are two processes of conditioning or only one is not a question about behavior, because the external contingencies in respondent and operant conditioning are clearly different.... The question is about a common process—an inferred mechanism" (p. 15).

The growing recognition that Pavlovian procedures can provide insight into instrumental behavior can be seen by comparing the old and new handbooks of operant behavior (Honig, 1966; Honig & Staddon, 1977). These two handbooks, published about a decade apart, present very different perspectives on operant–Pavlovian interactions. Honig's (1966) handbook contains no chapters on the issue, whereas that of Honig and Staddon (1977) contains three chapters that deal with the problem in detail (Blackman, 1977; Dunham, 1977; B. Schwartz & Gamzu, 1977). This reflects the increased theoretical importance of phenomena such as autoshaping and concerns over issues raised by biological constraints on learning, as well as a growing practical realization that many operant procedures may contain implicit Pavlovian contingencies and vice versa.

Many stimuli may serve as either operant or Pavlovian reinforcers, and factors that establish a stimulus as an effective reinforcer in one of these paradigms should also establish that stimulus as an effective reinforcer in the other paradigm. Catania (1971), in arguing for an operant–respondent continuum to replace the operant–respondent dichotomy, made a similar point about establishing operations: "most stimuli that are regarded as [operant] reinforcers have the property that the responses they elicit increase in probability with deprivation, and decrease in probability with successive presentations (satiation)" (p. 209). Glickman (1973) reached a similar conclusion when considering the issue from a biological constraints perspective: "From a naive evolutionary vantage point, stimuli that evoke vigorous consummatory activities *should* also produce approach or withdrawal behaviour and, in a plastic organism, *should* also have the capacity of modifying the probability of an arbitrary operant" (pp. 207–208).

Studies have shown that operant and Pavlovian contingencies can be used to condition the same response with the same reinforcer. Wahlsten and Cole (1972), for example, conditioned leg flexion in dogs with leg shock using both Pavlovian and omission contingencies. The pigeon's key peck is perhaps the best known example of a response that may be conditioned and maintained under either operant or Pavlovian contingencies using the same reinforcer (see reviews by Locurto, Terrace, & Gibbon, 1981; B. Schwartz & Gamzu, 1977; Tomie, Brooks, & Zito, 1989), but other "operant" responses (such as lever pressing in rats) have been conditioned with Pavlovian procedures (e.g., Boakes, 1977).

In cases in which data obtained with operant and Pavlovian procedures have been compared, the behavioral effect have often been qualitatively similar. Operant local contrast is similar to Pavlovian induction (Malone, 1976). Generalization gradients obtained with Pavlovian procedures are similar to those obtained with operant procedures (Parker, Serdikoff, Kaminski, & Critchfield, 1991; Weiss & Weissman, 1992). Stimulus control established with Pavlovian procedures facilitates the development of subsequent operant discrimination learning with the same stimuli (Bower & Grusec, 1964; Mellgren & Ost, 1969). Conditioned inhibition and blocking effects, which are typically studied with Pavlovian procedures, have also been obtained with operant procedures (Brown & Jenkins, 1967; Mackintosh & Honig, 1970), and blocking has been proposed as a factor in operant stimulus control (e.g., Fields, Bruno, & Keller, 1976; Williams, 1973, 1975). Prominent investigators have suggested that partial reinforcement effects are the only major learning phenomena with qualitatively different results in operant and Pavlovian studies (Catania, 1971; Terrace, 1973).

The operational distinction between operant and Pavlovian procedures, based on the presence versus absence of a response contingency, may still be maintained even if the same reinforcer is used in both cases. However, not all response-independent procedures are commonly described as Pavlovian in nature. Time-based schedules have been used to study superstition (Herrnstein, 1966) and schedule-induced behavior (Wetherington, 1982). Cohen and Looney (1984) addressed the difficulties in properly assessing reinforcement effects in some of these response-independent procedures. Cases in which operant and Pavlovian procedures result in differences in conditioned behavior may be more relevant to a discussion of the role of the response–reinforcer contingency than to a discussion of operant versus Pavlovian reinforcement. Use of variable- and fixed-interval reinforcement schedules results in markedly different response patterns, but the common interpretation is that the difference is due to differences in contingency, not to any fundamental differences in the nature of reinforcement. Reinforcement produces increases in conditioned behavior, whether through operant or Pavlovian contingencies. The reinforcer is still reinforcing, despite differences in response frequency or patterning. Operations that make reinforcers more or less effective should have similar effects across different sets of contingencies.

SEXUAL REINFORCEMENT

Response-contingent presentation of a female has been used to reinforce a variety of instrumental responses in male rats, including running (Beach & Jordan, 1956; Sheffield, Wulff, & Backer, 1951; Ware, 1968), crossing an electrified grid (Anderson, 1938), digging through sand (Anderson, 1938), and lever pressing (Everitt, Fray, Kostarczyk, Taylor, & Stacey, 1987; Everitt & Stacey, 1987; Jowaisas, Taylor, Dewsbury, & Malagodi, 1971; M. Schwartz, 1956). Response-contingent presentation of a female has also been used to reinforce running in male guinea pigs (Seward & Seward, 1940) and lever pressing in male rhesus monkeys (Michael & Keverne, 1968). Response-contingent presentation of a male has been used to reinforce lever pressing in female rats (Bermant, 1961; Bermant & Westbrook, 1966; French, Fitzpatrick, & Law, 1972) and lever pressing in female rhesus monkeys (Keverne, 1976). However, some response constraints on instrumental sexual conditioning have also been observed (Gilbertson, 1975; Sevenster, 1973).

Numerous examples of the effectiveness of sexual reinforcement have also been reported in studies that have employed Pavlovian conditioning procedures. Pavlovian procedures have resulted in conditioned approach and display behavior to localized conditioned stimuli (Domjan, Lyons, North, & Bruell, 1986; Hollis, Cadieux, & Colbert, 1989), conditioned sexual arousal (Zamble, Hadad, Mitchell, & Cutmore, 1985), and conditioned neuroendocrine changes (Graham & Desjardins, 1980).

In the present paper, we will discuss (a) response components of sexual reinforcement, (b) stimulus aspects of a reinforcing sexual partner, and (c) motivational substrates of sexual reinforcement.

Response Components of Sexual Reinforcement

Response components of sexual reinforcement were originally investigated by Sheffield et al. (1951) within the context of drive-reduction theories of reinforcement. According

to these theories, completed copulatory behavior is reinforcing because it reduces sexual drive. Sheffield et al. tested this prediction by providing male rats with access to a receptive female in the goal box of a runway apparatus. Upon reaching the goal box, the subjects were permitted to mount and intromit during interactions with the female, but they were not permitted to ejaculate. Contrary to predictions of drive-reduction theory, the subjects increased their running speed with repeated trials, even though the restriction on ejaculation presumably prevented reduction of their sex drive. Based on these results, Sheffield et al. concluded that drive reduction is not necessary for sexual reinforcement.

More recently, Gilbertson (1975) reinforced key pecking in male pigeons with courtship access to a female. Sevenster (1973) also used courtship access to a female, this time to reinforce swimming through a ring by male stickleback fish. Eliasson and Myerson (1975) reinforced running in female rats with noncopulatory exposure to a male rat.

Similar results have been obtained using Pavlovian procedures. Zamble et al. (1985) paired conditioned stimuli with exposure to a female rat on the other side of a wire screen and found that, for male rats, this resulted in a decreased latency to ejaculate during copulatory test trials conducted with the conditioned stimulus. Using blue gourami fish, Hollis et al. (1989) obtained conditioned approach and sexual displays by males to a light that preceded visual exposure to a female. Peele and Ferster (1982) reported conditioned key pecking in both male and female pigeons using an autoshaping procedure in which courtship opportunity served as the reinforcer. Crawford and Domjan (1993) observed conditioned approach by male quail to a localized conditioned stimulus that preceded visual exposure to a female, and this conditioned approach to the light was relatively insensitive to an omission procedure. Using a combined operant–Pavlovian procedure, Deni (1978) found that male, but not female, quail reduced their rate of food-reinforced key pecking when given visual exposure to a conspecific.

The above studies have demonstrated that exposure to a female without consummation of the sexual behavior sequence can serve as an effective reinforcer in a variety of species. However, other evidence has indicated that completion of copulation typically results in stronger reinforcement effects. Kagen (1955) tested independent groups of male rats in a T maze with a female presented as the reinforcer in one goal box and a stimulus male presented in the opposite goal box. One group of subjects was allowed to mount without intromission or ejaculation after each choice of the female side, another group was allowed to mount and intromit but not ejaculate, and a third group was allowed to copulate until ejaculation. The ejaculation group showed the most consistent choice of the female side of the maze. In a related study, Whalen (1961, Experiment 2) also used a T maze. A female rat was presented in one goal box, and the opposite goal box was empty. Male rats that were permitted to make one or four intromission responses on each trial developed a preference for the female side of the maze, and the group that received four intromissions developed faster running speeds than the group that received only one intromission per trial. For a third group of subjects, only mounting was possible because the female rat on the reinforced side of the T maze had its vagina surgically closed. The subjects in this group showed very little preference for the female side, and their running speeds decreased with successive conditioning trials.

Analogous results have been obtained using Pavlovian procedures. Holloway and Domjan (1993b) found that male quail that were allowed to copulate with a female acquired stronger approach to a conditioned stimulus that was paired with access to the female than did males that had the conditioned stimulus paired with only visual access to the female. Furthermore, male quail that were given visual access to a live female as the reinforcer showed more conditioned approach behavior than did males that were given visual exposure to a nonmoving taxidermic model of a female.

Sexually receptive female rats are also sensitive to the various stages of the copulatory response sequence. Females remain in the receptive lordosis posture longer when males copulate to ejaculation and engage in shorter bouts of lordosis when males mount but do not intromit (Kuehn & Beach, 1963). Peirce and Nuttall (1961) allowed sexually receptive female rats to choose how much time they spent in an arena with several sexually active males. The latencies of the females to return to the male arena varied as a function of the last

copulatory episode in the arena. Females returned to the male arena sooner following copulations without ejaculation than following copulations with ejaculation.

Similar results have been obtained with female rats that were trained to lever press for access to a male. The longest response latencies were obtained following copulations ending in ejaculation, intermediate latencies occurred after copulations that involved intromission without ejaculation, and the shortest latencies occurred following copulatory episodes that included only mounting (Bermant, 1961). In a subsequent experiment, Bermant and Westbrook (1966) reinforced lever pressing in female rats with one sexual contact (mount, intromission, or ejaculation) with a male. Response latencies were shortest following nonejaculatory contacts. Anesthetization of the vaginal area or copulation with males that had a normal ejaculatory reflex but did not deposit a sperm plug also resulted in short response latencies compared to control conditions. These data suggest that completion of the sexual behavior sequence is more reinforcing for both female and male rats than are partial copulations.

The above findings support the conclusion that the strength of sexual reinforcement is directly related to the extent to which subjects complete the copulatory behavior sequence. Other lines of evidence show that performance of the copulatory response sequence is itself subject to modification by learning. Kagen (1955) found that male rats that were permitted to intromit but not ejaculate during interactions with a receptive female decreased their copulatory attempts with successive trials. Kagen also found a decline in copulatory attempts in a group of male rats that was permitted to interact with females whose vaginas had been surgically closed. This finding was subsequently replicated by Whalen (1961, Experiment 1).

Conditioned changes in copulatory behavior have also been reported by Silberberg and Adler (1974), who used a differential reinforcement schedule to condition male rats to achieve ejaculation earlier in the copulatory response sequence. The subjects in the experimental group were allowed to intromit only seven times during each training session. This restriction resulted in the rats learning to achieve ejaculation with fewer intromissions than that observed in control groups that did not receive the response contingency.

Performance of the copulatory response sequence also can be altered by Pavlovian conditioning procedures. For example, Zamble et al. (1985) paired the placement of male rats in a plastic tub lined with wood shavings with exposure to a sexually receptive female on the other side of a wire screen. As a consequence of this conditioning procedure, the subjects ejaculated more quickly in test sessions with a female rat after being placed in the plastic tub than did control subjects that received unpaired exposure to the plastic tub and the female. Using blue gourami fish, Hollis et al. (1989) paired exposure to a red light with visual exposure to a female, and found that when the males were given copulatory access to females, the red light facilitated courtship appeasement behavior and suppressed aggressive responses. In a similar study conducted with male Japanese quail, Domjan et al. (1986) found that the latency of copulatory behavior was shorter following exposure to a red light that had been paired with copulatory access to a female quail than following exposure to a light that was unpaired with access to a female.

Conditioned contextual cues can also facilitate copulatory behavior. Domjan, Greene, and North (1989) gave one group of male quail opportunities to copulate with a female in a large test chamber; another group of males received copulatory opportunities in smaller wire-mesh home cages. During subsequent test sessions, the males were allowed to copulate with a taxidermic model that contained the head and neck of a female quail. Subjects that previously copulated with live females in the test arena were more likely to copulate with the test model than were the control group. Sexual conditioning of contextual cues has also been observed to facilitate copulatory behavior in male rats (Zamble, Mitchell, & Findlay, 1986).

Stimulus Aspects of a Reinforcing Sexual Partner

The stimulus aspects of a reinforcing sexual partner may be influenced by ontogenetic experience to varying degrees in different species. For some species, recognition of a potential sexual partner is largely independent of early social experience. For example, brood parasites (such as cowbirds) are raised by a host

species and do not see other conspecifics until maturity. Therefore, their mate recognition cannot be based on early social experience (West, King, & Eastzer, 1981). In other species, early social experience can significantly influence later copulatory behavior and mate preference. Social deprivation in infancy can result in deficient adult social and sexual behavior in rhesus monkeys (Mason, 1960). In some bird species, early social experience with particular types of birds can bias later mate choice in favor of those types of individuals, as evidenced by the phenomenon of sexual imprinting (see reviews by Bateson, 1978; Hess, 1973). In an interesting form of sexual imprinting, Fillion and Blass (1986) found that adult male rats ejaculated more quickly during copulation with a female if the female was treated with an odor the males encountered during suckling in infancy. Imprinting can also result in the stimulus control of sexual behavior by highly atypical stimuli. Hediger (1964), for example, cited several instances of zoo animals that came to react to specific keepers as either potential mates or sexual rivals. These responses are also sometimes seen in pets or laboratory animals that develop social attachments to humans (e.g., Beach, 1948).

Social contact with conspecifics or imprinted targets is reinforcing for young animals. Quail chicks will run on a treadmill to maintain proximity to similar-aged chicks (Launay, Mills, & Faure, 1991), and Peterson (1960) trained ducklings to peck a response key using the presentation of an imprinting stimulus as a reinforcer. Young animals are clearly unable to engage in adult sexual behavior, but the fact that they undergo sexual imprinting suggests that these cases of social reinforcement can have a sexual component.

Animals can also learn about potential sexual partners as adults. Successful copulations may bring behavior under the stimulus control of features of potential sexual partners that do not control behavior initially. These stimulus features may then serve as conditioned reinforcers in their own right. Conversely, animals may learn to decrease responding to stimulus features of inappropriate sexual partners from exposure to these stimuli in the absence of sexual reinforcement. Both of these forms of learning have been demonstrated in a variety of species.

Male quail in reproductive condition will approach and remain near visible, but inaccessible, females. This approach behavior is facilitated by copulatory experience with the type of female that is seen (Domjan & Hall, 1986a; Nash, Domjan, & Askins, 1989), even if that female is different from the type the male was exposed to during its usual period of sexual imprinting (Nash & Domjan, 1991). An intact male quail can also come to approach and remain near a functionally castrated male if the intact subject receives repeated copulatory opportunities with the functionally castrated male (Nash & Domjan, 1991).

Even arbitrary stimulus features can become effective sexual reinforcers through association with copulatory opportunity. Domjan et al. (1988) used exposure to a female quail adorned with bright orange feathers as a signal for the opportunity to copulate with a normal female. This conditioning procedure increased the frequency of copulatory responses that were directed toward the adorned female during a postconditioning test session. In another study, Domjan, McDonald, and Holloway (1992) gradually covered the natural plumage of a taxidermic female model with terrycloth and successfully transferred stimulus control of male copulation to an artificial model that was completely covered with terrycloth.

A common related finding in mammalian species is that sexual experience increases the preference of males for the odor of receptive as compared to nonreceptive females (see Taylor & Dewsbury, 1990, for a review). This effect has been reported in male beagles (Doty & Dunbar, 1974), mice (Hayashi & Kimura, 1974), rats (Carr, Loeb, & Dissinger, 1965; Lydell & Doty, 1972; Pfaff & Pfaffman, 1969; Stern, 1970), and monkeys (Goldfoot, 1981).

Whereas copulatory experience increases the reinforcing efficacy of particular stimulus features of potential sexual partners, in certain circumstances noncopulatory exposure serves to decrease reinforcement efficacy. This is particularly evident in how males learn to discriminate the gender of other members of their own species. Males of several species, including ring doves (Barfield, 1971), mice (Nyby, Bigelow, Kerchner, & Barbenhenn, 1983), ruffed grouse (Allen, 1934), red-winged blackbirds (Noble & Vogt, 1935), and Japanese quail (Sachs, 1966; Schlinger, Palter, & Callard, 1987) initially respond similarly to male and female conspecifics. In these species, males

have to learn to discriminate males from females.

Studies with Japanese quail have shown that with differential sexual reinforcement, males learn to discriminate the gender of other quail. For example, pairing exposure to female quail with copulatory opportunity and providing exposure to male stimulus birds in the absence of sexual reinforcement results in more approach to female stimulus birds than to male birds (Domjan & Hall, 1986a; Domjan & Ravert, 1991; Nash et al., 1989). If copulatory opportunity is given with functionally castrated male stimulus birds and the subjects are exposed to female birds without copulatory opportunity, then the male subject will come to approach male stimulus birds more than females (Nash & Domjan, 1991). However, these effects are obtained only with sexually naive males. Following a history of copulation with female quail, males continue to approach and remain near females even if they are no longer allowed to copulate with them (Domjan & Hall, 1986a; Nash & Domjan, 1991). In contrast, approach to males is much more susceptible to extinction if exposure to stimulus males is no longer paired with copulatory opportunity (Nash & Domjan, 1991). Male quail may have a biological predisposition to approach female cues more than male cues. This predisposition may be manifest in faster conditioning of female cues or greater resistance of female cues to extinction. Alternatively, copulatory access to males and females may provide qualitatively different types of reinforcement. Males that attempt to copulate with other males are often rebuffed. Even if the target male is somewhat cooperative, as were the functionally castrated males in the study by Nash and Domjan (1991), the subject male is unlikely to be properly stimulated to ejaculation.

Motivational Substrates of Sexual Reinforcement

Perhaps the most important motivational factor in the performance of sexually reinforced behavior, whether the behavior is the product of operant or Pavlovian conditioning procedures, is the hormonal status of the subjects. In male Japanese quail, the initial development of sexual behavior is correlated with a rapid increase in plasma testosterone (Ottinger & Brinkley, 1978). Adult male testosterone levels are sensitive to daily photostimulation. Restriction of the daily light cycle causes regression of the testes and reduction in plasma testosterone (Delville, Sulon, & Balthazart, 1985; Follet & Farner, 1966; Sachs, 1967; Siopes & Wilson, 1975). The reduction in testosterone results in decreased copulatory behavior (Adkins & Adler, 1972; Sachs, 1969). Males on restricted photoperiods also cease to approach and remain near females (Domjan, 1987). All of these effects can be reversed by hormone replacement therapy. Similar hormone–behavior relationships have been obtained in rodent species. Beach and Holz-Tucker (1949), for example, found that the copulatory behavior of castrated male rats was related to the dose of testosterone that was administered.

Early evidence of the dependence of sexually reinforced instrumental behavior on sexual motivation was provided by Beach and Jordan (1956), who trained male rats to run a straight alley for access to a receptive female. Each day, trials were continued until copulation resulted in ejaculation. After 17 days of training, the running speed of the subjects increased sixfold. With subsequent castration, running speeds slowed to pretraining levels. However, when testosterone replacement therapy was provided, the subjects returned to running as fast as they did at the end of training.

Similar results have been obtained in a free-operant paradigm by Everitt and Stacey (1987) using a second-order schedule of sexual reinforcement. In the terminal second-order schedule, lever pressing was reinforced on a fixed-ratio 10 schedule by a 1-s presentation of a light. The first completion of the fixed-ratio requirement after 15 min produced both the light and opportunity to copulate with a female rat. Following training on this second-order schedule, castration produced a significant decline in lever-press responding. However, responding was restored when exogenous testosterone was provided.

The instrumental behavior of females is similarly affected by hormonal state. Keverne (1976) used copulatory access to a male monkey to reinforce bar pressing by female rhesus monkeys on a fixed-ratio schedule. Response rates varied directly with the menstrual cycle of the females. In addition, latency to complete the fixed ratio increased after ovariectomy and decreased following hormone replacement

treatment. Eliasson and Myerson (1975) found that during estrous periods, female rats ran to a male stimulus rat in preference to a female stimulus rat with which they could not copulate. This preference was lost during pregnancy but began to reemerge during the later stages of lactation. French et al. (1972) gave female rats a choice between two males as sexual reinforcement. Stable preferences for a particular male developed when the females were in estrus but not when they were in diestrus.

Sexual motivation is also important for the performance of conditioned behavior that results from Pavlovian reinforcement procedures. In studies with male Japanese quail, Holloway and Domjan (1993a) found that conditioned approach to a stimulus paired with copulatory opportunity declined when subjects were placed on a restricted light schedule that was insufficient to maintain gonadal testosterone production. However, return to sufficient photostimulation and testosterone replacement therapy both produced recovery in the conditioned approach behavior.

The rate of decline in male sexual behavior that results from castration shows substantial individual variation in some species (Hart, 1974). Furthermore, this individual variation may be related to the prior sexual experience of the subjects. Rosenblatt and Aronson (1958) found, for example, that prior sexual experience slowed postcastration decline in sexual behavior in male cats. Larsson (1978) found similar effects with male rats.

Prior sexual experience can also reduce the deleterious effects of sensory deficits on sexual behavior. Some sensory information is necessary for normal male sexual behavior. Penile desensitization or deafferentation disrupts copulation by male rats (Carlsson & Larsson, 1964; Lodder, 1976) and cats (Aronson & Cooper, 1968, 1969). This disruption is lessened by prior sexual experience (Lodder, 1976). Other sensory deficits also impair sexual performance by males. Beach (1942) found that sexually experienced male rats copulated more normally after the imposition of sensory deficits than did sexually inexperienced males.

CONCLUDING COMMENTS

Much of the research we have discussed has involved the use of male subjects. In cases in which the sexual behavior of females has been studied, it has often been more difficult to obtain evidence of sexual reinforcement. Female quail, for example, did not approach and remain near visible males (Domjan & Hall, 1986b) and did not alter their rate of food-reinforced pecking when shown conspecifics (Deni, 1978). For these reasons, attempts to demonstrate sexual learning in female quail have been problematic.

Gender differences in learning are probably strongly influenced by the mating system of the species (Domjan & Hollis, 1988). Trivers (1972) argued that which gender (male or female) has the greater role in mate selection will depend on which makes the greater parental investment in the offspring in terms of gamete production, parental care, territorial defense, and other factors. The gender making the lesser parental investment usually competes for mates. This may lead to sexually dimorphic differences in the speed of acquisition of sexually conditioned responses, differences in asymptotic performance, or differences in the kinds of sexual learning that may occur (Domjan & Hollis, 1988).

Sexual reinforcers are distinct from more typical reinforcers (e.g., food or water) in that they are different for males and females, differ as a function of species and mating system, and show ontogenetic and seasonal changes. These differences make sexual reinforcement a good choice to study the generality of learning and reinforcement effects. Although many aspects of sexual reinforcement remain to be investigated, the effects obtained to date have been similar to those observed with more conventional reinforcers. Orderly acquisition effects have been obtained with both instrumental and Pavlovian procedures (e.g., Everitt et al., 1987; Hollis et al., 1989). Extinction effects (Domjan et al., 1986; Zamble et al., 1986), latent inhibition (Zamble et al., 1986), second-order conditioning (Zamble et al., 1985), and discrimination learning (Domjan et al., 1988; Nash et al., 1989; Nash & Domjan, 1991) all have been obtained with sexual reinforcement. And, as in autoshaping with food reinforcement, the use of an omission contingency does not eliminate or preclude the development of conditioned approach behavior (Crawford & Domjan, 1993). These similarities extend the generality of findings obtained with more conventional reinforcers, but future research on

gender and species differences may yet reveal evidence of adaptive specializations with sexual reinforcement.

REFERENCES

Adkins, E. K., and Adler, N. T. (1972). Hormonal control of behavior in the Japanese quail. *Journal of Comparative and Physiological Psychology, 81,* 27–36.

Allen, A. A. (1934). Sex rhythm in the ruffed grouse (*Bonasa umbellus* Linn.) and other birds. *Auk, 51,* 180–199.

Allison, J. (1989). The nature of reinforcement. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning and the impact of biological constraints on learning* (pp. 13–39). Hillsdale, NJ: Erlbaum.

Anderson, E. E. (1938). The interrelationship of drives in the male albino rat. *Comparative Psychology Monographs, 14* (6, Serial No. 72).

Aronson, L. R., & Cooper, M. L. (1968). Desensitization of the glans penis and sexual behavior in cats. In M. Diamond (Ed.), *Reproduction and sexual behavior* (pp. 51–82). Bloomington: Indiana University Press.

Aronson, L. R., & Cooper, M. L. (1969). Mating behaviour in sexually inexperienced cats after desensitization of the glans penis. *Animal Behaviour, 17,* 208–212.

Barfield, R. J. (1971). Activation of sexual and aggressive behavior by androgen implanted into the male ring dove brain. *Endocrinology, 89,* 1470–1476.

Bateson, P. P. G. (1978). Early experience and sexual preferences. In J. B. Hutchison (Ed.), *Biological determinants of sexual behaviour* (pp. 29–53). Chichester, England: Wiley.

Beach, F. A. (1942). Analysis of the stimuli adequate to elicit mating behavior in the sexually inexperienced male rat. *Journal of Comparative Psychology, 33,* 163–207.

Beach, F. A. (1948). Sexual behavior in animals and man. *Harvey Lectures, 43,* 254–280.

Beach, F. A., & Holz-Tucker, A. M. (1949). Effects of different concentrations of androgen upon sexual behavior in castrated male rats. *Journal of Comparative Psychology, 42,* 433–453.

Beach, F. A., & Jordan, L. (1956). Effects of sexual reinforcement upon the performance of male rats in a straight runway. *Journal of Comparative and Physiological Psychology, 49,* 105–110.

Bermant, G. (1961). Response latencies of female rats during sexual intercourse. *Science, 133,* 1771–1773.

Bermant, G., & Westbrook, W. H. (1966). Peripheral factors in the regulation of sexual contact by female rats. *Journal of Comparative and Physiological Psychology, 61,* 244–250.

Blackman, D. (1977). Conditioned suppression and the effects of classical conditioning on operant behavior. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 340–363). Englewood Cliffs, NJ: Prentice-Hall.

Boakes, R. A. (1977). Performance on learning to associate a stimulus with positive reinforcement. In H. Davis & H. M. B. Hurwitz (Eds.), *Operant–Pavlovian interactions* (pp. 67–97). Hillsdale, NJ: Erlbaum.

Bolles, R. C. (1985). The slaying of Goliath: What happened to reinforcement theory. In T. D. Johnston & A. T. Pietrewicz (Eds.), *Issues in the ecological study of learning* (pp. 387–399). Hillsdale, NJ: Erlbaum.

Bower, G., & Grusec, T. (1964). Effect of prior Pavlovian discrimination training upon learning an operant discrimination. *Journal of the Experimental Analysis of Behavior, 7,* 401–404.

Brown, P. L., & Jenkins, H. M. (1967). Conditioned inhibition and excitation in operant discrimination learning. *Journal of Experimental Psychology, 75,* 255–266.

Carlsson, S. G., & Larsson, K. (1964). Mating in male rats after local anesthetization of the glans penis. *Zeitschrift für Tierpsychologie, 21,* 854–856.

Carr, W. J., Loeb, L. S., & Dissinger, M. L. (1965). Responses of rats to sex odors. *Journal of Comparative and Physiological Psychology, 59,* 370–377.

Catania, A. C. (1971). Elicitation, reinforcement, and stimulus control. In R. Glaser (Ed.), *The nature of reinforcement* (pp. 196–220). New York: Academic Press.

Cohen, P. S., & Looney, T. A. (1984). Induction by reinforcer schedules. *Journal of the Experimental Analysis of Behavior, 41,* 345–353.

Crawford, L., & Domjan, M. (1993). Sexual approach conditioning: Omission contingency tests. *Animal Learning & Behavior, 21,* 42–50.

Delville, Y., Sulon, J., & Balthazart, J. (1985). Hormonal correlates of gonadal regression and spontaneous recovery in Japanese quail exposed to short day-lengths. *Archives Internationales de Physiologie et de Biochimie, 93,* 123–133.

Deni, R. (1978). Social influences on operant behavior in Japanese quail: Sex differences among subjects, and sex and age differences among companions. *Psychological Record, 28,* 95–108.

Domjan, M. (1987). Photoperiodic and endocrine control of social proximity behavior in male Japanese quail (*Coturnix coturnix japonica*). *Behavioral Neuroscience, 101,* 385–392.

Domjan, M., & Galef, B. G., Jr. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Animal Learning & Behavior, 11,* 151–161.

Domjan, M., Greene, P., & North, N. C. (1989). Contextual conditioning and the control of copulatory behavior by species-specific sign stimuli in male Japanese quail. *Journal of Experimental Psychology: Animal Behavior Processes, 15,* 147–153.

Domjan, M., & Hall, S. (1986a). Determinants of social proximity in Japanese quail (*Coturnix coturnix japonica*): Male behavior. *Journal of Comparative Psychology, 100,* 59–67.

Domjan, M., & Hall, S. (1986b). Sexual dimorphism in the social proximity behavior of Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology, 100,* 68–71.

Domjan, M., & Hollis, K. L. (1988). Reproductive behavior: A potential model system for adaptive specializations in learning. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 213–237). Hillsdale, NJ: Erlbaum.

Domjan, M., Lyons, R., North, N. C., & Bruell, J. (1986). Sexual Pavlovian conditioned approach behavior in male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology, 100,* 413–421.

Domjan, M., McDonald, M., & Holloway, K. (1992). Conditioning copulatory behavior to an artificial object: Efficacy of stimulus fading. *Animal Learning & Behavior, 20,* 350–362.

Domjan, M., O'Vary, D., & Greene, P. (1988). Conditioning of appetitive and consummatory sexual behavior in male Japanese quail. *Journal of the Experimental Analysis of Behavior, 50,* 505–519.

Domjan, M., & Ravert, R. D. (1991). Discriminating the sex of conspecifics by male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology, 105,* 157–164.

Doty, R. L., & Dunbar, I. (1974). Attraction of beagles to conspecific urine, vaginal and anal sac secretion odors. *Physiology & Behavior, 12,* 825–833.

Dunham, P. (1977). The nature of reinforcing stimuli. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 98–124). Englewood Cliffs, NJ: Prentice-Hall.

Eliasson, M., & Meyerson, B. J. (1975). Sexual preference in female rats during estrous cycle, pregnancy and lactation. *Physiology & Behavior, 14,* 705–710.

Everitt, B. J., Fray, P., Kostarczyk, E., Taylor, S., & Stacey, P. (1987). Studies of instrumental behavior with sexual reinforcement in male rats (*Rattus norvegicus*): I. Control by brief visual stimuli paired with a receptive female. *Journal of Comparative Psychology, 101,* 395–406.

Everitt, B. J., & Stacey, P. (1987). Studies of instrumental behavior with sexual reinforcement in male rats (*Rattus norvegicus*): II. Effects of preoptic area lesions, castration, and testosterone. *Journal of Comparative Psychology, 101,* 407–419.

Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement.* New York: Appleton-Century-Crofts.

Fields, L., Bruno, V., & Keller, K. (1976). The stages of acquisition in stimulus feeding. *Journal of the Experimental Analysis of Behavior, 26,* 295–300.

Fillion, T. J., & Blass, E. M. (1986). Infantile experience with suckling odors determines adult sexual behavior in male rats. *Science, 231,* 729–731.

Follett, B. K., & Farner, D. S. (1966). The effects of daily photoperiod on gonadal growth, neurohypophysial hormone content, and neurosecretion in the hypothalamo-hypophysial system of the Japanese quail (*Coturnix coturnix japonica*). *General and Comparative Endocrinology, 7,* 111–124.

French, D., Fitzpatrick, D., & Law, O. T. (1972). Operant investigation of mating preference in female rats. *Journal of Comparative and Physiological Psychology, 81,* 226–232.

Gilbertson, D. W. (1975). Courtship as a reinforcement for key pecking in the pigeon, *Columba livia. Animal Behaviour, 23,* 735–744.

Glickman, S. E. (1973). Responses and reinforcement. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning: Limitations and predispositions* (pp. 207–241). London: Academic Press.

Goldfoot, D. A. (1981). Olfaction, sexual behavior, and the pheromone hypothesis in rhesus monkeys: A critique. *American Zoologist, 21,* 153–164.

Graham, J. M., & Desjardins, C. (1980). Classical conditioning: Induction of luteinizing hormone and testosterone secretion in anticipation of sexual activity. *Science, 210,* 1039–1041.

Hanson, S. J., & Timberlake, W. (1983). Regulation during challenge: A general model of learned performance under schedule constraint. *Psychological Review, 90,* 261–282.

Hart, B. L. (1974). Gonadal androgen and sociosexual behavior of male mammals: A comparative analysis. *Psychological Bulletin, 81,* 383–400.

Hayashi, S., & Kimura, T. (1974). Sex attractant emitted by female mice. *Physiology & Behavior, 13,* 563–567.

Hediger, H. (1964). *Wild animals in captivity.* New York: Dover.

Herrnstein, R. J. (1966). Superstition: A corollary of the principles of operant conditioning. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 33–51). New York: Appleton-Century-Crofts.

Hess, E. H. (1973). *Imprinting: Early experience and the developmental psychobiology of attachment.* New York: Van Nostrand Reinhold.

Hinde, R. A., & Stevenson-Hinde, J. (Eds.). (1973). *Constraints on learning: Limitations and predispositions.* London: Academic Press.

Hollis, K. L., Cadieux, E. L., & Colbert, M. M. (1989). The biological function of Pavlovian conditioning: A mechanism for mating success in the blue gourami (*Trichogaster trichopterus*). *Journal of Comparative Psychology, 103,* 115–121.

Holloway, K. S., & Domjan, M. (1993a). Sexual approach conditioning: Unconditioned stimulus devaluation using hormone manipulations. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 47–55.

Holloway, K. S., & Domjan, M. (1993b). Sexual approach conditioning: Unconditioned stimulus factors. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 38–46.

Honig, W. K. (Ed.). (1966). *Operant behavior: Areas of research and application.* New York: Appleton-Century-Crofts.

Honig, W. K., & Staddon, J. E. R. (1977). Introduction. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 1–6). Englewood Cliffs, NJ: Prentice-Hall.

Hull, C. L. (1943). *Principles of behavior.* New York: Appleton-Century-Crofts.

Jowaisas, D., Taylor, J., Dewsbury, D. A., & Malagodi, E. F. (1971). Copulatory behavior of male rats under an imposed operant requirement. *Psychonomic Science, 25,* 287–290.

Kagen, J. (1955). Differential reward value of incomplete and complete sexual behavior. *Journal of Comparative and Physiological Psychology, 48,* 59–64.

Keverne, E. B. (1976). Sexual receptivity and attractiveness in the female rhesus monkey. In J. S. Rosenblatt, R. A. Hinde, E. Shaw, & C. Beer (Eds.), *Advances in the study of behavior* (Vol. 7, pp. 155–200). New York: Academic Press.

Kuehn, R. E., & Beach, F. A. (1963). Quantitative measurement of sexual receptivity in female rats. *Behaviour, 21,* 282–299.

Larsson, K. (1978). Experiential factors in the development of sexual behavior. In J. B. Hutchison (Ed.), *Biological determinants of sexual behavior* (pp. 55–86). New York: Wiley.

Launay, F., Mills, A. D., & Faure, J. M. (1991). Social motivation in Japanese quail *Coturnix coturnix japonica* chicks selected for high or low levels of treadmill behaviour. *Behavioural Processes, 24,* 95–110.

Lea, S. E. G. (1978). The psychology and economics of demand. *Psychological Bulletin, 85,* 441–466.

Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist, 14,* 163–176.

Locurto, C. M., Terrace, H. S., & Gibbon J. (Eds.). (1981). *Autoshaping and conditioning theory.* New York: Academic Press.

Lodder, J. (1976). Penile deafferentation and the effect of mating experience on sexual motivation in adult male rats. *Physiology & Behavior, 17,* 571–573.

Lydell, K., & Doty, R. L. (1972). Male rat odor preferences for female urine as a function of sexual experience, urine age, and urine source. *Hormones and Behavior, 3,* 205–212.

Mackintosh, N. J., & Honig, W. K. (1970). Blocking and enhancement of stimulus control in pigeons. *Journal of Comparative and Physiological Psychology, 73,* 78–85.

Malone, J. C., Jr. (1976). Local contrast and Pavlovian induction. *Journal of the Experimental Analysis of Behavior, 26,* 425–440.

Mason, W. A. (1960). The effects of social restriction on the behavior of rhesus monkeys: I. Free social behavior. *Journal of Comparative and Physiological Psychology, 53,* 582–589.

McCann, T. S. (1981). Aggression and sexual activity of male southern elephant seals, *Mirounga leonina. Journal of Zoology, 195,* 295–310.

Mellgren, R. L., & Ost, J. W. P. (1969). Transfer of Pavlovian differential conditioning to an operant discrimination. *Journal of Comparative and Physiological Psychology, 67,* 390–394.

Michael, R. P., & Keverne, E. B. (1968). Pheromones in the communication of sexual status in primates. *Nature, 218,* 746–749.

Nash, S., & Domjan, M. (1991). Learning to discriminate the sex of conspecifics in male Japanese quail (*Coturnix coturnix japonica*): Tests of biological constraints. *Journal of Experimental Psychology: Animal Behavior Processes, 17,* 342–353.

Nash, S., Domjan, M., & Askins, M. (1989). Sexual-discrimination learning in male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology, 103,* 347–358.

Noble, G. K., & Vogt, W. (1935). An experimental study of sex recognition in birds. *Auk, 52,* 278–286.

Nyby, J., Bigelow, J., Kerchner, M., & Barbehenn, F. (1983). Male mouse (*Mus musculus*) ultrasonic vocalizations to female urine: Why is heterosexual experience necessary? *Behavioral and Neural Biology, 38,* 32–46.

Ottinger, M. A., & Brinkley, H.J. (1978). Testosterone and sex-related behavior and morphology: Relationship during maturation and in the adult Japanese quail. *Hormones and Behavior, 11,* 175–182.

Parker, B. K., Serdikoff, S. L., Kaminski, B. J., & Critchfield, T. S. (1991). Stimulus control of Pavlovian facilitation. *Journal of the Experimental Analysis of Behavior, 55,* 275–286.

Peele, D. B., & Ferster, C. B. (1982). Authoshaped key pecking maintained by access to a social space. *Journal of the Experimental Analysis of Behavior, 38,* 181–189.

Peirce, J. T., & Nuttall, R. L. (1961). Self-paced sexual behavior in the female rat. *Journal of Comparative and Physiological Psychology, 54,* 310–313.

Peterson, N. (1960). Control of behavior by presentation of an imprinted stimulus. *Science, 132,* 1395–1396.

Pfaff, D., & Pfaffmann, C. (1969). Behavioral and electrophysiological responses of male rats to female rat urine odors. In C. Pfaffmann (Ed.), *Olfaction and taste* (Vol. 3, pp. 258–267). New York: Rockefeller University Press.

Rosenblatt, J. S., & Aronson, L. R. (1958). The decline of sexual behavior in male cats after castration with special reference to the role of prior sexual experience. *Behaviour, 12,* 285–338.

Sachs, B. D. (1966). Sexual-aggressive interactions among pairs of quail (*Coturnix coturnix japonica*). *American Zoologist, 6,* 559.

Sachs, B. D. (1967). Photoperiodic control of the cloacal gland of the Japanese quail. *Science, 157,* 201–203.

Sachs, B. D. (1969). Photoperiod control of reproductive behavior and physiology of the male Japanese quail (*Coturnix coturnix japonica*). *Hormones and Behavior, 1,* 7–24.

Schlinger, B. A., Palter, B., & Callard, G. V. (1987). A method to quantify aggressiveness in Japanese quail (*Coturnix coturnix japonica*). *Physiology and Behavior, 40,* 343–348.

Schwartz, B., & Gamzu, E. (1977). Pavlovian control of operant behavior: An analysis of autoshaping and its implications for operant conditioning. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 53–97). Englewood Cliffs, NJ: Prentice-Hall.

Schwartz, M. (1956). Instrumental and consummatory measures of sexual capacity in the male rat. *Journal of Comparative and Physiological Psychology, 49,* 328–333.

Seligman, M. E. P., & Hager, J. L. (Eds.). (1972). *Biological boundaries of learning.* Englewood Cliffs, NJ: Prentice-Hall.

Sevenster, P. (1973). Incompatability of response and reward. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning: Limitations and predispositions* (pp. 265–283). London: Academic Press.

Seward, J. P., & Seward, G. H. (1940). Studies on the reproductive activities of the guinea pig: IV. A comparison of sex drive in males and females. *Journal of Genetic Psychology, 57,* 429–440.

Sheffield, F. D., Wulff, J. J., & Backer, R. (1951). Reward value of copulation without sex drive reduction. *Journal of Comparative and Physiological Psychology, 44,* 3–8.

Silberberg, A., & Adler, N. (1974). Modulation of the copulatory sequence of the male rat by a schedule of reinforcement. *Science, 185,* 374–376.

Siopes, T. D., & Wilson, W. O. (1975). The cloacal gland: An external indicator of testicular development in *Coturnix. Poultry Science, 54,* 1225–1229.

Skinner, B. F. (1983). Can the experimental analysis of behavior rescue psychology? *Behavior Analyst, 6,* 9–17.

Stern, J. J. (1970). Responses of male rats to sex odors. *Physiology & Behavior, 5,* 519–524.

Taylor, S. A., & Dewsbury, D. A. (1990). Male preferences for females of different reproductive conditions: A critical review. In D. W. Macdonald, D. Müller-Schwarze, & S. E. Natynczuk (Eds.), *Chemical signals in vertebrates* (pp. 184–198). Oxford: Oxford University Press.

Terrace, H. S. (1973). Classical conditioning. In J. A. Nevin (Ed.), *The study of behavior: Learning, motivation,*

emotion, and instinct (pp. 70–112). Glenview, IL: Scott, Foresman.

Tomie, A., Brooks, W., & Zito, B. (1989). Sign-tracking: The search for reward. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Pavlovian conditioning and the status of traditional learning theory* (pp. 191–223). Hillsdale, NJ: Erlbaum.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago: Aldine.

Wahlsten, D. L., & Cole, M. (1972). Classical and avoidance training of leg flexion in the dog. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 379–408). New York: Appleton-Century-Crofts.

Ware, R. (1968). Development of differential reinforcing values of sexual responses in the male albino rat. *Journal of Comparative and Physiological Psychology, 65,* 461–465.

Weiss, S. J., & Weissman, R. D. (1992). Generalization peak shift for autoshaped and operant key pecks. *Journal of the Experimental Analysis of Behavior, 57,* 127–143.

West, M. J., King, A. P., & Eastzer, D. H. (1981). The cowbird: Reflections on development from an unlikely source. *American Scientist, 69,* 56–66.

Wetherington, C. L. (1982). Is adjunctive behavior a third class of behavior? *Neuroscience and Biobehavioral Reviews, 6,* 329–350.

Whalen, R. E. (1961). Effects of mounting without intromission and intromission without ejaculation on sexual behavior and maze learning. *Journal of Comparative and Physiological Psychology, 54,* 409–415.

Williams, B. A. (1973). The failure of stimulus control after presence-absence discrimination of click-rate. *Journal of the Experimental Analysis of Behavior, 20,* 23–27.

Williams, B. A. (1975). The blocking of reinforcement control. *Journal of the Experimental Analysis of Behavior, 24,* 215–225.

Zamble, E., Hadad, G. M., Mitchell, J. B., & Cutmore, T. R. H. (1985). Pavlovian conditioning of sexual arousal: First- and second-order effects. *Journal of Experimental Psychology: Animal Behavior Processes, 11,* 598–610.

Zamble, E., Mitchell, J. B., & Findlay, H. (1986). Pavlovian conditioning of sexual arousal: Parametric and background manipulations. *Journal of Experimental Psychology: Animal Behavior Processes, 12,* 403–411.